WIND POLLINATION IN AQUATIC ANGIOSPERMS

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ABSTRACT

Aquatic angiosperms have evolved from terrestrial ancestors several times. About 79 angiosperm families and 380 genera contain aquatic species; 119 genera (31.3%) are wind pollinated. Among these wind-pollinated aquatics, 100 genera have obvious terrestrial relatives that are also wind pollinated. Sixteen genera (4.2%) have no obvious terrestrial relatives but belong to exclusively anemophilous families; the anemophily, however, could be associated with life in water. In only two genera (0.5%), Brasenia (Cabombaceae) and Limnobium (Hydrocharitaceae), is it likely that the evolution from entomophily to anemophily has taken place in the aquatic environment. In Hydrilla (Hydrocharitaceae) the pollen grains are heavy and are propelled through air from the male to the female; although this mechanism almost certainly evolved in water, it is not considered to be true anemophily where buoyant grains are carried by air movements. Wind pollination is not considered an important feature especially associated with life in the aquatic environment.

Crane (1986) suggested that the seeming simplicity of wind pollination has deflected interest in a process that is, in fact, far from straightforward. However, combining the detailed pioneer work on pollen dimensions and pollen production by Pohl (1937a, b) with the physical approaches by Whitehead (1969) and Niklas (1985) and with the renewed morphological approach of Crane (1986), a better view of wind pollination in gymnosperms and terrestrial angiosperms is emerging. Wind pollination and associated characteristics have rarely been studied in aquatic angiosperms.

The main purpose of this review is to collect information bearing on the question of which aquatic plants are pollinated by wind. By comparing these with their terrestrial ancestors it should be possible to find out which of them have modified their pollination mechanisms. In turn, this should give insight into the question: is wind pollination especially associated with the aquatic environment? Perhaps the highest development of aquatic angiosperms is the use of water for the transfer of pollen (hydrogamy). It is also an aim of this review to see if wind pollination is a prerequisite to hydrogamy.

The term aquatic is used in the sense described by Cook et al. (1974); it includes plants whose photosynthetically active parts are submerged in water or floating on the water surface permanently or, at least, for several months each year. Within the angiosperms the aquatics have evolved from terrestrial ancestors several times, as Sculthorpe (1967) pointed out. It is important to appreciate that most aquatic angiosperms resemble terrestrial flowering plants, not only in gross features of floral morphology, but also in exhibiting similar trends of floral specialization. The aquatic members of predominantly anemophilous families Centrolepidaceae, Cyperaceae, Hydatellaceae, Juncaceae, and Poaceae from the point of view of their pollination biology resemble the terrestrial members and are thus not described in detail here.

The first angiosperms were almost certainly insect pollinated, so anemophily is a derived state (for example, see Crane, 1986). It is also clear that wind pollination has originated several times from diverse stocks. Anemophily has evolved at different times from different morphological backgrounds with differing degrees of efficiency. It is not surprising that it is sometimes difficult to make a clear-cut distinction between wind-pollinated plants and those pollinated by other means. Many predominantly wind-pollinated species may be regularly visited by pollen-eating insects (particularly syrphid flies) and may occasionally be pollinated by insects. For such plants Stelleman (1984) used the term ambophily.

Quantitative data on the efficiency of wind pollination or even direct observations are lacking among aquatics. The decision of whether a species is wind pollinated or not is often based on morphological criteria. This is justifiable since there is a whole complex of characters associated with anemophily. The following list attempts to summarize the most important features of this wind pollination syndrome.

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1. The characteristics of wind-borne pollen grains are well summarized by Crane (1986): size 20–40(–60) µm diam., Reynolds number around 0.1 at a terminal velocity of 5 cm sec.$^{-1}$, spread singly, powdery and nonsticky (lipids absent, chemically altered or hidden within the wall), surface relatively smooth, resistant to changes in temperature and to desiccation (size and/or number of apertures reduced).

2. The flowers are usually unisexual: the male must dispense pollen, and the female must catch pollen.

3. The amount of pollen is increased: this is usually achieved by an increase in anther size and is often associated with a decrease in number of anthers in each flower and an increase in number of male flowers.

4. The flowers are usually separated from the leaves (temporally or spatially) and held above the water on specialized structures.

5. The perianth and bracts are reduced (to increase aerodynamic efficiency).

6. There are sometimes special arresting or explosive mechanisms to ensure that pollen gets into the airstream.

7. The number of ovules in each flower is usually reduced; the reason for this is not clear.

8. The stigmas are often specialized to increase "capture" efficiency.

I. Aquatics Previously Considered Anemophilous but Probably Entomophilous

Details of the pollination mechanisms of many aquatic angiosperms are unknown. Many with small and insignificant flowers have been considered to be wind or even water pollinated. The following, which have been thought to be wind pollinated, are probably pollinated by other means; all are illustrated in Cook et al. (1974).

ALISMATACEAE

Ten of the eleven genera have large showy petals; some are scented and have septal nectaries and are clearly insect pollinated. *Wiesneria*, a genus with two African and one Asian species, recently redescribed by Sivadasan (1986), has whorled, subsessile, unisexual flowers with small and reflexed perianths. The male flowers, which are borne above the females, have three stamens, the lowest number in the family. The carpels are reduced to three or four in each female flower. These characters may suggest anemophily, but the inflorescences are shorter than and partly hidden by the leaves; the petals, though small, are cream-colored and relatively conspicuous; the anthers are small (ca. 1 mm long); the filaments are short (ca. 0.5 mm long); the pollen grains are echinate, have numerous apertures (Fig. 6), and are somewhat sticky. These characters strongly suggest insect pollination. It is not known if *Wiesneria* is scented or if it produces nectar.

APONOGETONACEAE

Aponogeton, the only genus, sometimes has catkinlike inflorescences. A few species have unisexual flowers, and sometimes the perianth is reduced. These features suggest wind pollination. However, the pollen has supratectal spines in all species (see Bruggen, 1985) and most species investigated to date have septal nectaries and are strongly scented. *Aponogeton* is insect pollinated, but in some species some pollen may be transferred by wind. This is unlikely, however, as the pollen grains stick together in clumps.

ARACEAE

It has been suggested that *Acorus* and *Orontium* are wind pollinated. A considerable amount of work has been published on both genera, cited by Cook et al. (1974), but I have found no observational data on pollination. From their morphology (mostly bisexual flowers, relatively large perianth segments, small anthers, sticky pollen) they are probably entomophilous.

ERIOCAULACEAE

Because the flowers are small, rather insignificant, often unisexual, and apparently dry, they have been considered to be wind pollinated. However, the flowers are structurally complex and elaborate. In the few species examined, they secrete nectar, have sticky pollen, and are thus most likely insect pollinated or autogamous (see Stützel, 1981, 1984).

HANGUANACEAE

The flowers are small and unisexual with long slender filaments, which suggests anemophily (see Dahlgren et al., 1985). However, the pollen grains are spinulose, the male flowers have conspicuous fleshy bodies, and the stigmas are not exposed beyond the perianth, all of which suggests zoogamy. No direct observations on pollination have yet been reported.
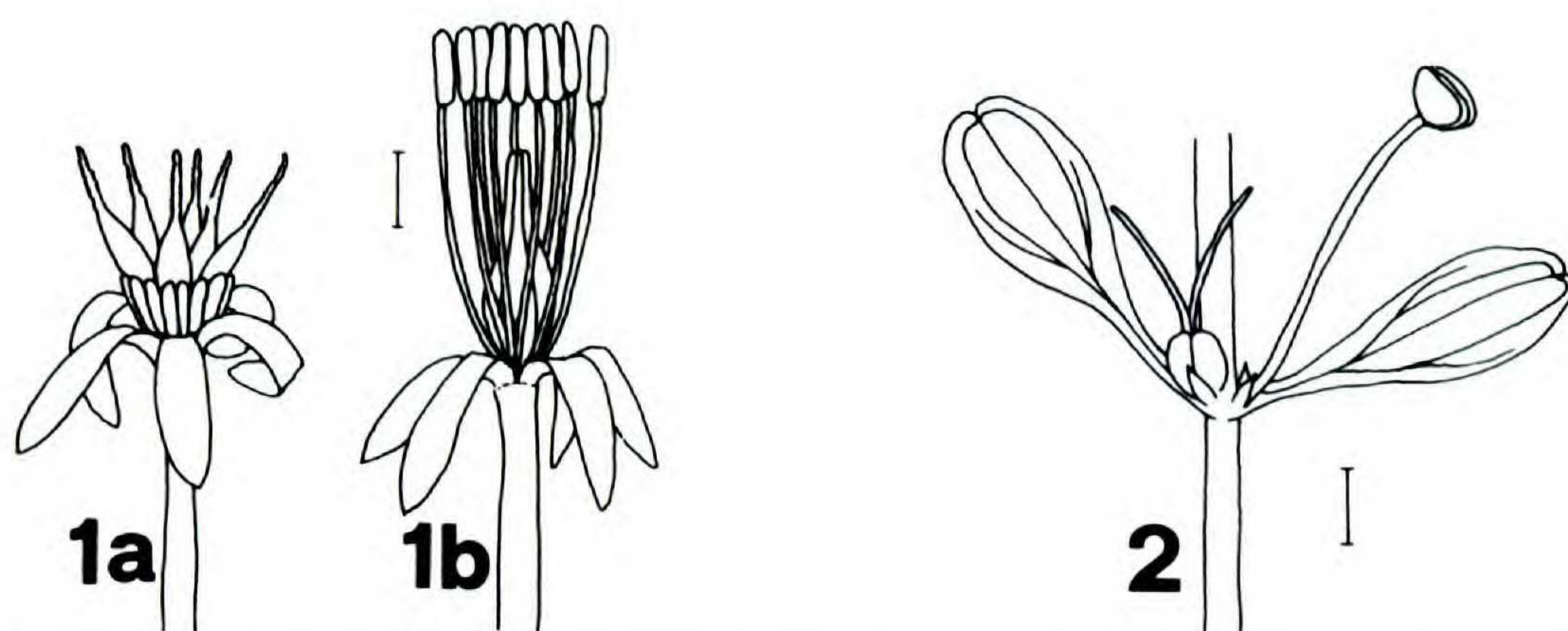
FIGURES 1, 2.   *1. Diagram of flowers of* Brasenia schreberi. *(a) Female phase. (b) Male phase. Scale bar = 6 mm.—2. Diagram of flowers of* Callitriche obtusangula. *Left, female flower. Right, male flower. Scale bar = 1 mm.*

LEMNACEAE

The flowers are unisexual, very small (stamens ca. 1 mm long, stigma ca. 0.5 mm above the carpel) and not obviously showy. Wind and water have been suggested as pollen vectors, but as Landolt (1986) pointed out, this is unlikely, as the pollen grains are spiny, sticky, often less than 20 μm in diameter, and sometimes only 20 grains develop in each locule; these characters all suggest zoogamy. Although water movements may bring flowers on different fronds in contact, the pollen is probably mostly transferred on the legs of different kinds of arthropods (flies, aphids, mites, small spiders). At least some races of *Lemna minor* and *Wolffiella oblonga* are self-incompatible, while many other species are self-compatible, although some of these are not autogamous and require a pollinator (for details see Landolt, 1986).

PODOSTEMACEAE

This family has about 45 genera, of which some, such as *Mourera* and *Tulasneantha*, are clearly insect pollinated. The majority, however, have very small, almost naked flowers (see Cook et al., 1974). Of these, some are probably autogamous, while others may well be wind pollinated (see Philbrick, 1984b). It is a shame that so little is known about the floral biology of this rather extraordinary family.

II. FAMILIES WITH WIND-POLLINATED SPECIES

CABOMBACEAE (sometimes included within the NYMPHAEACEAE)

Cabomba is insect pollinated, and *Brasenia* is wind pollinated (Fig. 1; see Osborn & Schneider, this volume: 778–794). *Brasenia* has most likely evolved to anemophily from entomophily in the aquatic milieu.

CALLITRICHACEAE

This monotypic family is wind pollinated (Fig. 2) or shows an extreme kind of autogamy above or below the water surface, described by Schotsman (1982, 1985) and Philbrick (1984a). It is doubtful that true hypohydrogamy (transfer of wet pollen through water to wet stigmas) takes place. It is also unlikely that epihydrogamy, with floating pollen, is an effective means of pollen transfer since the stigmas are usually either submerged or aerial.

HALORAGACEAE

Haloragis, Laurembergia, Myriophyllum, Proserpinaca, and *Vinkia* have aquatic species, all of which are well adapted to wind pollination. All have flowers with reduced and often caducous perianths (Fig. 3) and dry, powdery pollen liberated from long-filamented anthers. There is a trend from bisexual to unisexual flowers culminating in dioecy. Patten (1956) suggested without quantitative data that significant quantities of pollen may be transferred by insects in *Myriophyllum spicatum*.

HIPPURIDACEAE

This monotypic family has highly reduced bisexual or sometimes unisexual flowers. The stamens are reduced to one with a relatively massive anther, and the ovary is reduced to a virtually naked, one-seeded carpel (Fig. 4). The pollen is anemophilous-like. No published data on pollination have been found, but from personal observations it is strongly protogynous (Fig. 4), and seed-set is usually good. I can only assume it is wind pollinated.
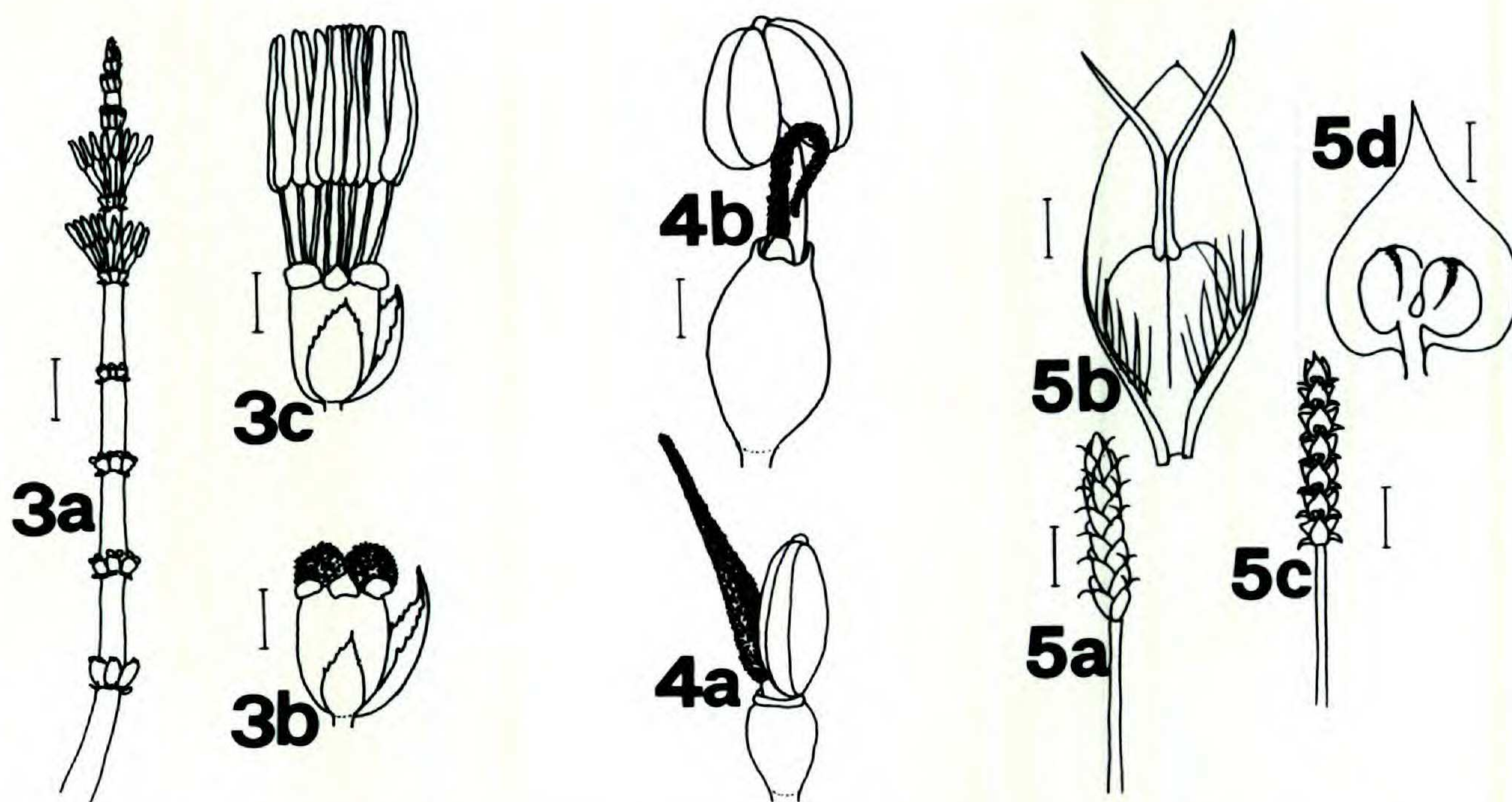
FIGURES 3–5. 3. *Diagrammatic representation of* Myriophyllum spicatum. *(a) Inflorescence, male above, female below. Scale bar = 1 cm. (b) Female flower. (c) Male flower. Scale bar = 1 mm.—4. Diagram of flowers of* Hippuris vulgaris. *(a) Female phase. (b) Male phase. Scale bar = 0.75 mm.—5. Diagrammatic representation of* Hydrostachys perrieri. *(a) Female inflorescence. Scale bar = 1 cm. (b) Female flower. Scale bar = 1 mm. (c) Male inflorescence. Scale bar = 1 cm. (d) Male flower. Scale bar = 1 mm.*

HYDROCHARITACEAE

This exclusively aquatic family with 16 genera is extraordinary in its spectrum of floral structures, showing entomophily, anemophily, epi- and hypohydrophily (see Cook, 1982, for a general review). In *Appertiella, Enhalus, Lagarosiphon* (Figs. 7, 11), *Maidenia, Nechamandra,* and *Vallisneria* (Fig. 8) the male flowers become detached from the mother plant and are dispersed by wind or water currents; in these genera the pollen is sticky and transferred directly from anther to stigma. In *Elodea* the pollen is liberated on the surface of the water (Fig. 12) and is dispersed by wind or water currents to the stigma (Cook & Urmi-König, 1985). Although wind plays an important role in pollination, this kind of pollination is usually classified as epihydrophilous, since part of the pollen is in contact with water; however, it must be stressed that the pollen and stigma remain dry.

In pollination biology *Hydrilla* is remarkable, as shown by Cook & Lüönd (1982). The male flowers are liberated from the mother plant as buds, which then open explosively, shooting pollen grains through the air. The pollen of *Hydrilla* is inaperturate (the furrow illustrated by Yeo et al., 1984, is an artifact), spherical, 93 ± 5.7 μm in diameter, and densely covered with baculae 2 μm long, each bearing a small flamelike process (Fig. 9a, b). This pollen is too large and rough to "fit" in the wind

pollination syndrome. The stigmas are rather small and borne at the base of a wineglasslike perianth (Fig. 10) exposed to the air but below the surface of the water. For effective pollination the pollen should not get into the airstream, as in other anemophilous plants, but must drop almost vertically to reach the stigmas, and it must stick and not bounce out again. The pollen is propelled through the air, but wind, as such, plays an unimportant role; I hope it is not necessary to create a new term for this unique pollination mechanism.

Described in detail by Cook & Urmi-König (1983), pollination in *Limnobium* is "normal" when compared with other genera of the Hydrocharitaceae. The sepals of the male flowers act as pollen-arresting organs (Fig. 13). The pollen is then "picked up" off the petals by the wind. The arched petals were suggested by Cook & Urmi-König (1983) to have an aerodynamic function, but after observations in the field it seems clear that their function is to keep the pollen dry when waves come or when it rains; when the flowers are immersed in water the sepals come to rest on the petals, thus enclosing an air bubble.

The marine genera *Halophila* and *Thalassia* have wettable pollen and stigmas and are pollinated underwater (hypohydrogamous).

Within the Hydrocharitaceae, *Limnobium* is the only genus with dry, powdery, and buoyant pollen that is transported to the stigmas by movements
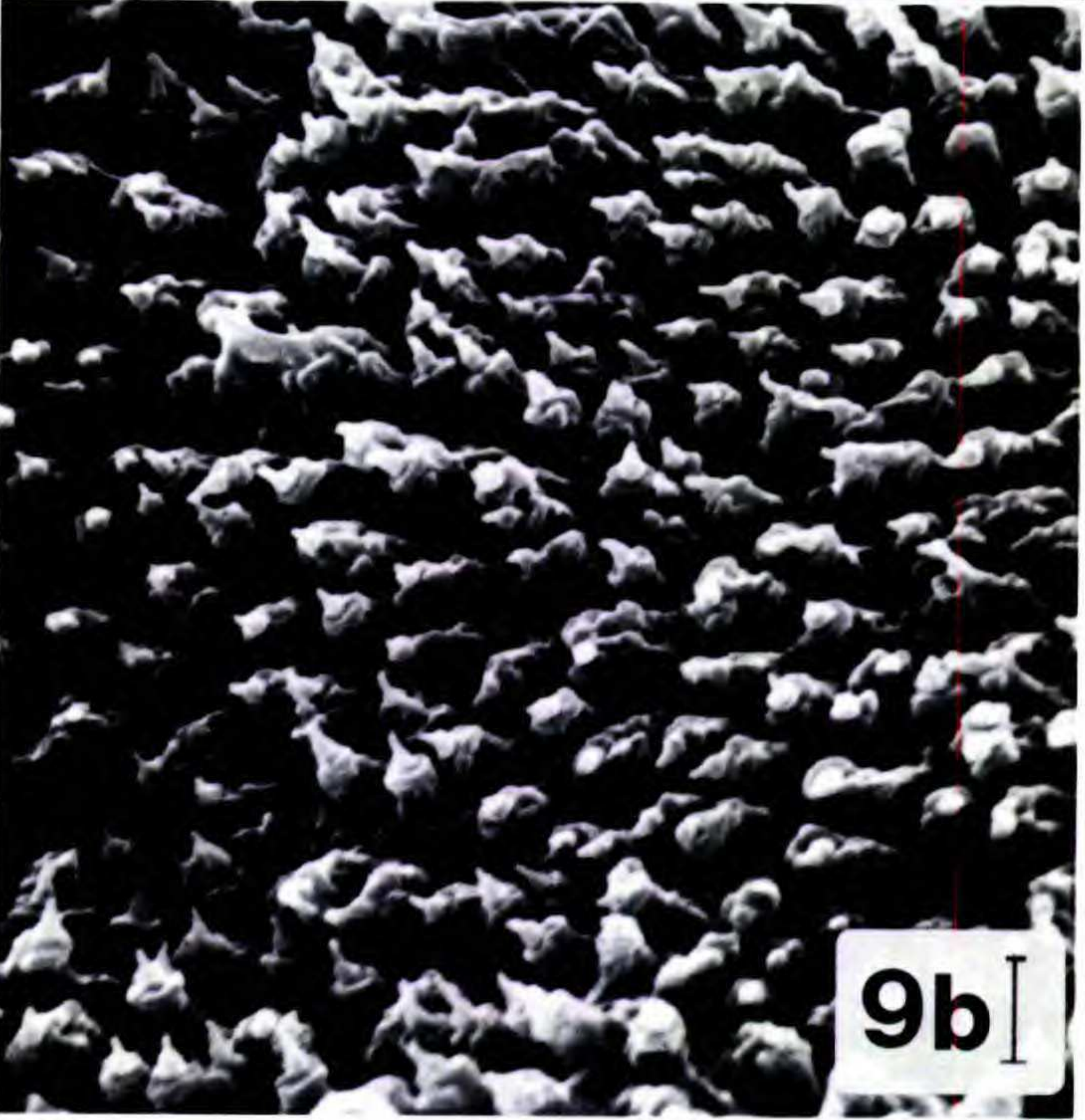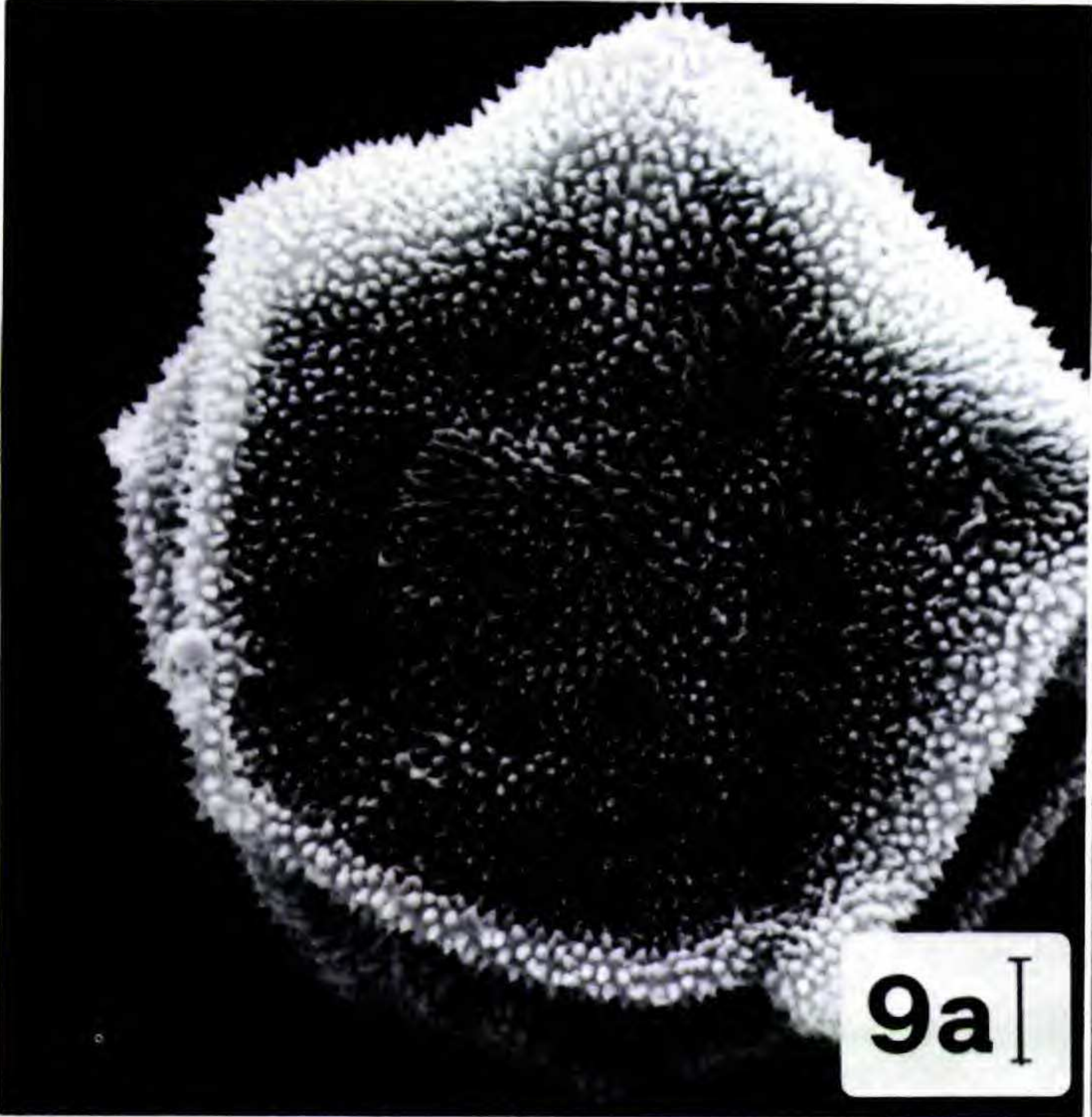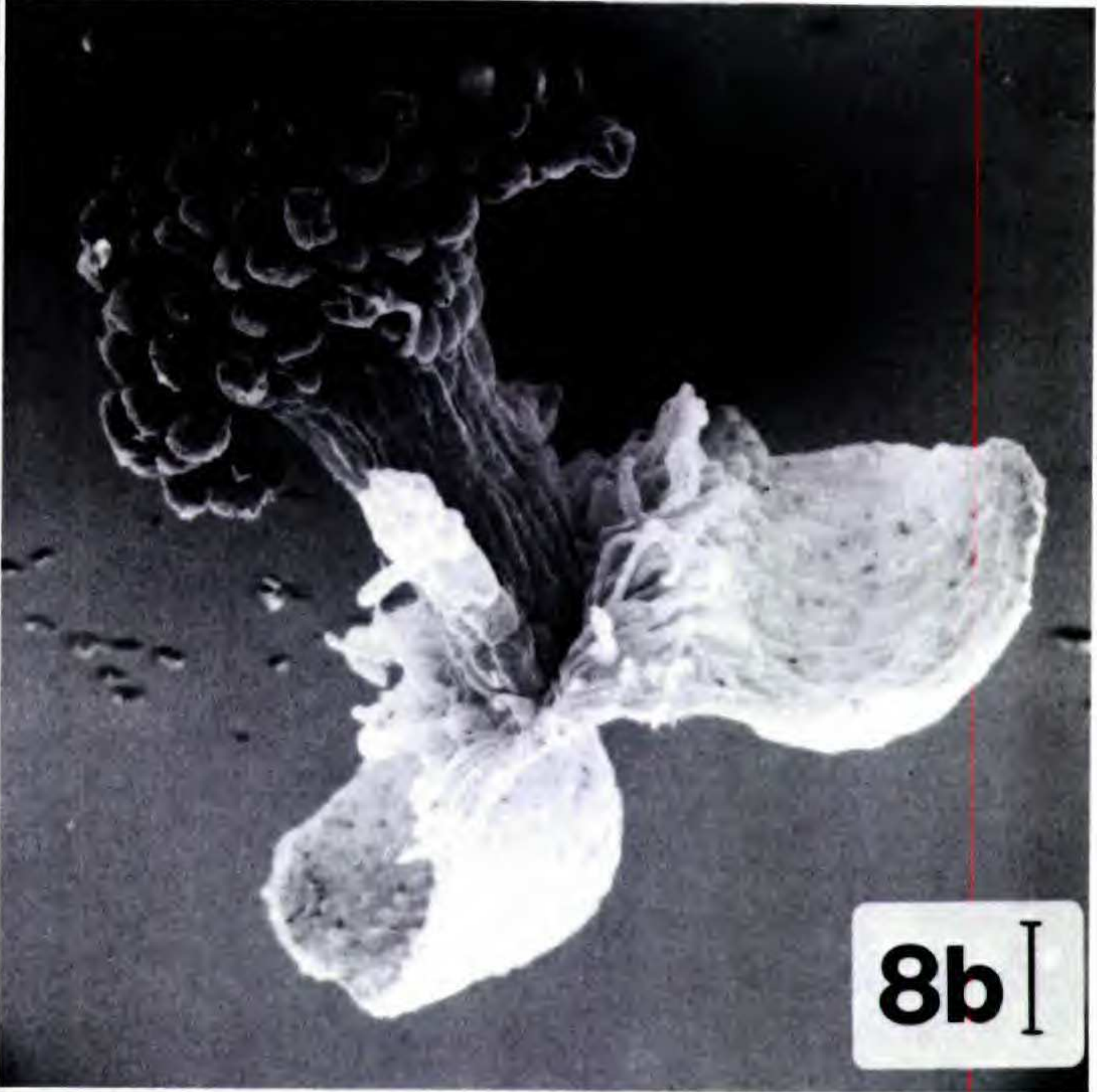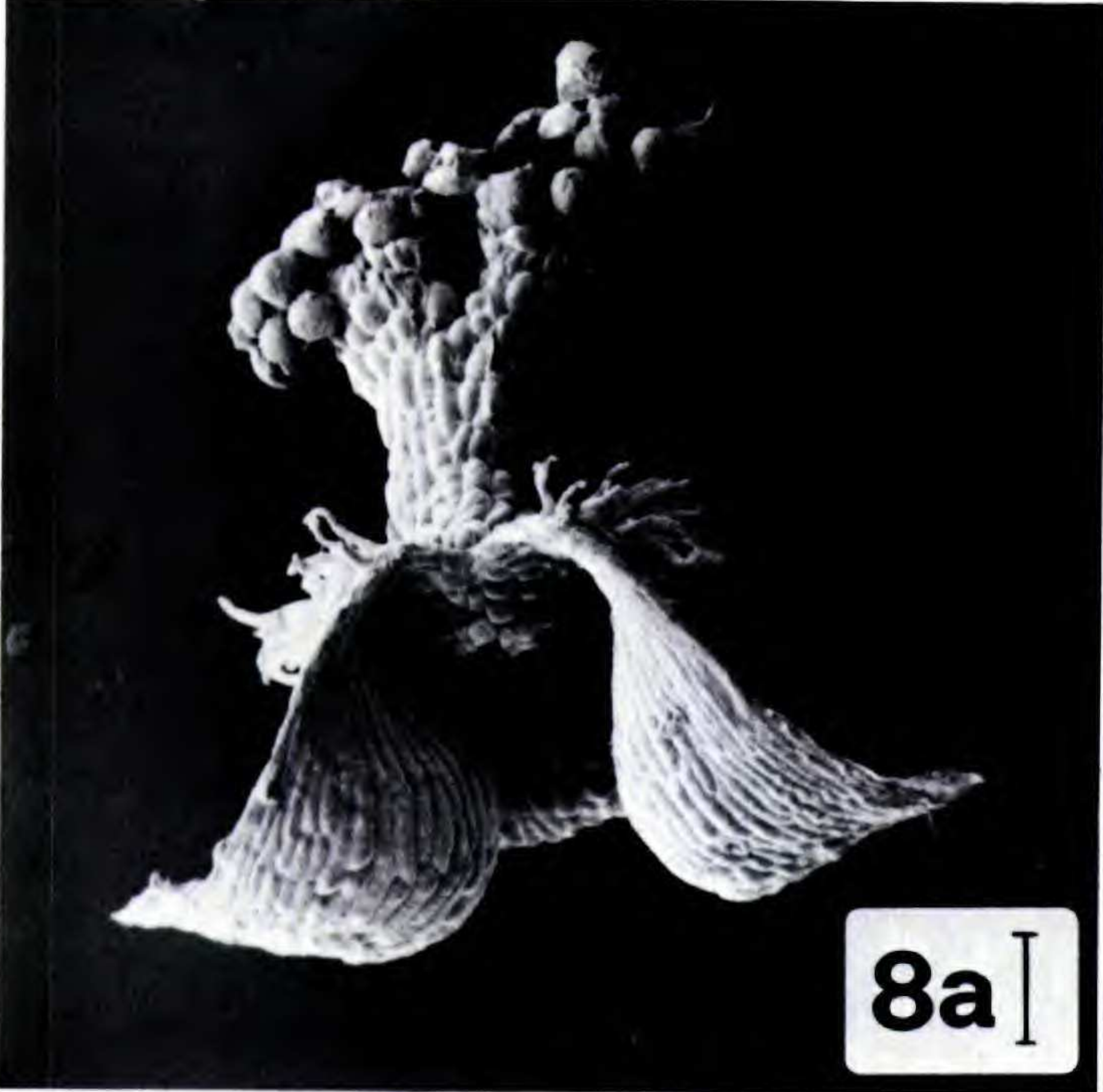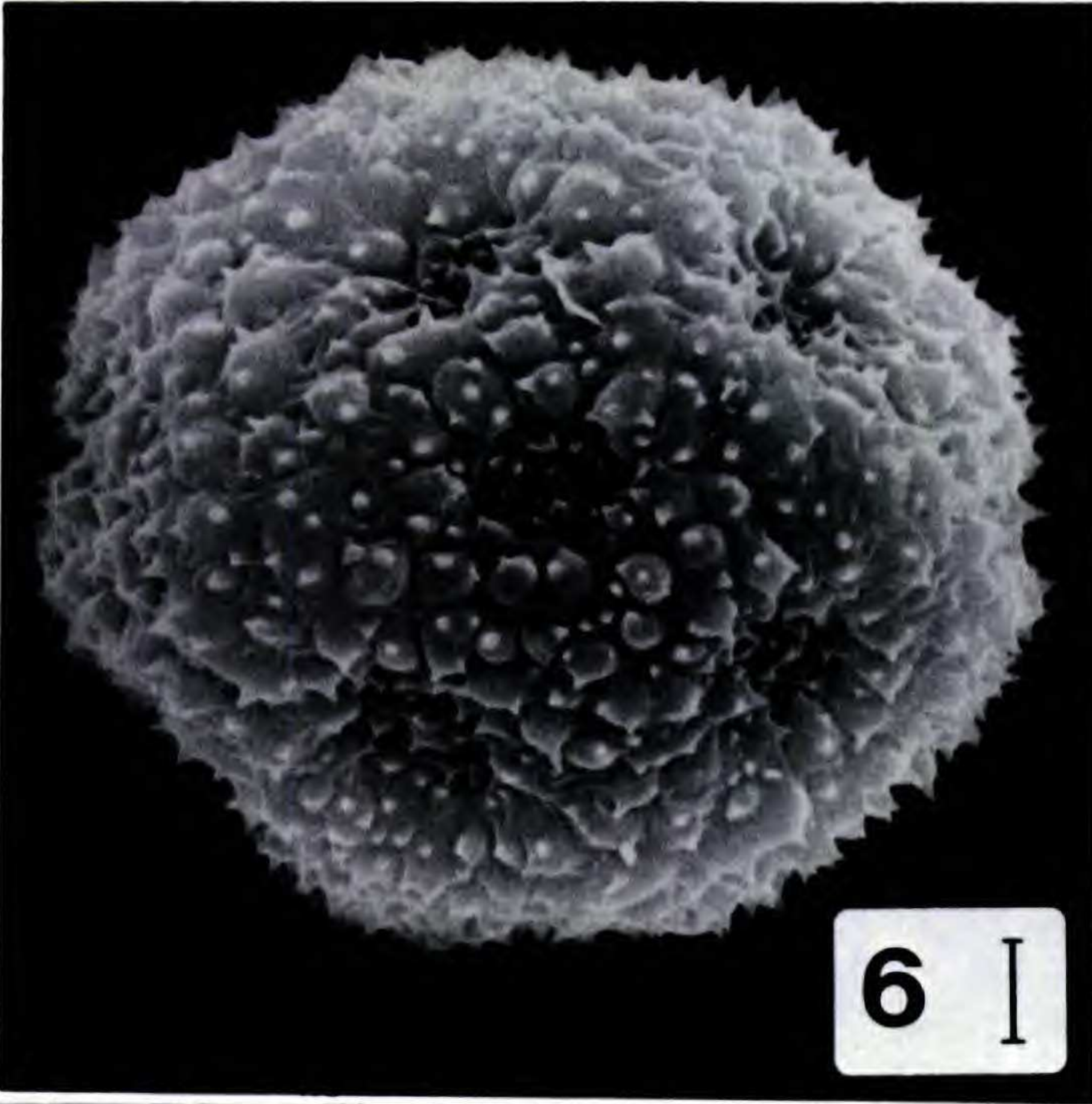
of air and thus can be called anemophilous. *Hydrilla* has heavy pollen actively propelled through the air and is not dependent on air movements; it is, therefore, not strictly speaking "wind pollinated." Morphological and anatomical evidence indicates that the patristic relationships of *Limnobium* are to exclusively entomophilous genera *Hydrocharis*, *Ottelia*, and *Stratiotes*. The epi- and hypohydrogamous genera (within the framework of the Hydrocharitaceae) are not patristically close to *Limnobium* and are probably derived from a *Blyxa*-like ancestor. The genus *Blyxa* is essentially entomophilous or highly autogamous (Cook et al., 1981; Cook & Lüönd, 1983).

The evolution from entomophily to anemophily in *Limnobium* has most likely taken place within the aquatic environment. The expanded sepals, which hold pollen until wind carries it off, and the arched petals, which protect the pollen from waves and submergence, may be considered as elaborations connected with wind pollination and with the aquatic environment.

HYDROSTACHYDACEAE

This extraordinary monotypic family, reviewed by Cusset (1973), has about 22 species. The morphology of the flowers suggests anemophily (Fig. 5). The perianth is absent and a bract arrests the pollen, analogous to *Limnobium*. The carpel contains numerous seeds, an unusual feature in anemophily. No direct observations on pollination have been published.

JUNCAGINACEAE and LILAEACEAE

These two families are sometimes united. From the floral morphology they are wind pollinated, but I know of no direct observations. Some species have pollen-arresting mechanisms very like those in *Potamogeton*, and others have highly heteromorphic flowers (Fig. 14) (Posluszny et al., 1986).

PLANTAGINACEAE

The aquatic genus *Littorella* has obvious affinities to the terrestrial genera *Bougneria* and *Plantago*. Some species of *Plantago* show tendencies toward entomophily, but most are anemophilous. *Littorella*, however, shows further anemophilous

specialization in having stalked male flowers and sessile, uniovulate female flowers.

POTAMOGETONACEAE and RUPPIACEAE

These two families are sometimes united. Most of the species of *Potamogeton* are wind pollinated, with erect, many-flowered spikes, spherical pollen grains, bisexual flowers with strong protogyny, and organs generally known as connective appendages to arrest the pollen and liberate it in the airstream after the female receptive phase (Fig. 15). *Potamogeton filiformis*, *P. pectinatus*, and others are pollinated below the water surface. This kind of pollination is described by Philbrick in this volume (pp. 836–841).

The pollination mechanism of *Groenlandia* has not, I believe, been critically described, but my own observations revealed that in spite of having rather short-stalked, two-flowered inflorescences, it is either autogamous or pollinated by wind and does not seem to be, as sometimes supposed, pollinated by floating pollen (epihydrogamous).

Ruppia is better known than the other genera; Verhoeven (1979) described the pollination in *R. cirrhosa* and *R. maritima* in detail. Both have curious elongated 'v'-shaped pollen grains (Fig. 16) that sometimes form chains. This might suggest hypohydrogamy, but the pollen is nonwettable and is liberated in bubbles; the stigmas are protected by the same bubbles. *Ruppia cirrhosa* is usually pollinated at the surface like *Elodea*, while *R. maritima*, in Europe, is usually pollinated in bubbles under water like *Potamogeton pectinatus*.

SPARGANIACEAE

A monotypic family having flowers arranged in unisexual heads with male heads above females (Fig. 17). All species are clearly wind pollinated (Cook & Nicholls, 1986, 1987), in spite of the fact that some syrphid flies specialize on *Sparganium* pollen as a source of food.

THURNIACEAE

It is not certain that this monotypic family deserves to be called aquatic. The floral structure suggests pollination by wind (Fig. 18) but no observations have been published.


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FIGURES 6–9. *6. Pollen grain of* Wiesneria triandra. *Scale bar = 5 μm.—7. Young male flower of* Lagarosiphon muscoides, *filaments and staminodes not fully extended and some pollen grains missing. Scale bar = 200 μm.— 8. The male flower of* Vallisneria americana. *(a) Showing branched stamen. (b) The same from the other side, showing tepal. Scale bar = 100 μm.—9. Pollen of* Hydrilla verticillata. *(a) A somewhat shrunken grain; when fresh they are spherical. Scale bar = 10 μm. (b) Detail of surface showing baculae. Scale bar = 2 μm.*
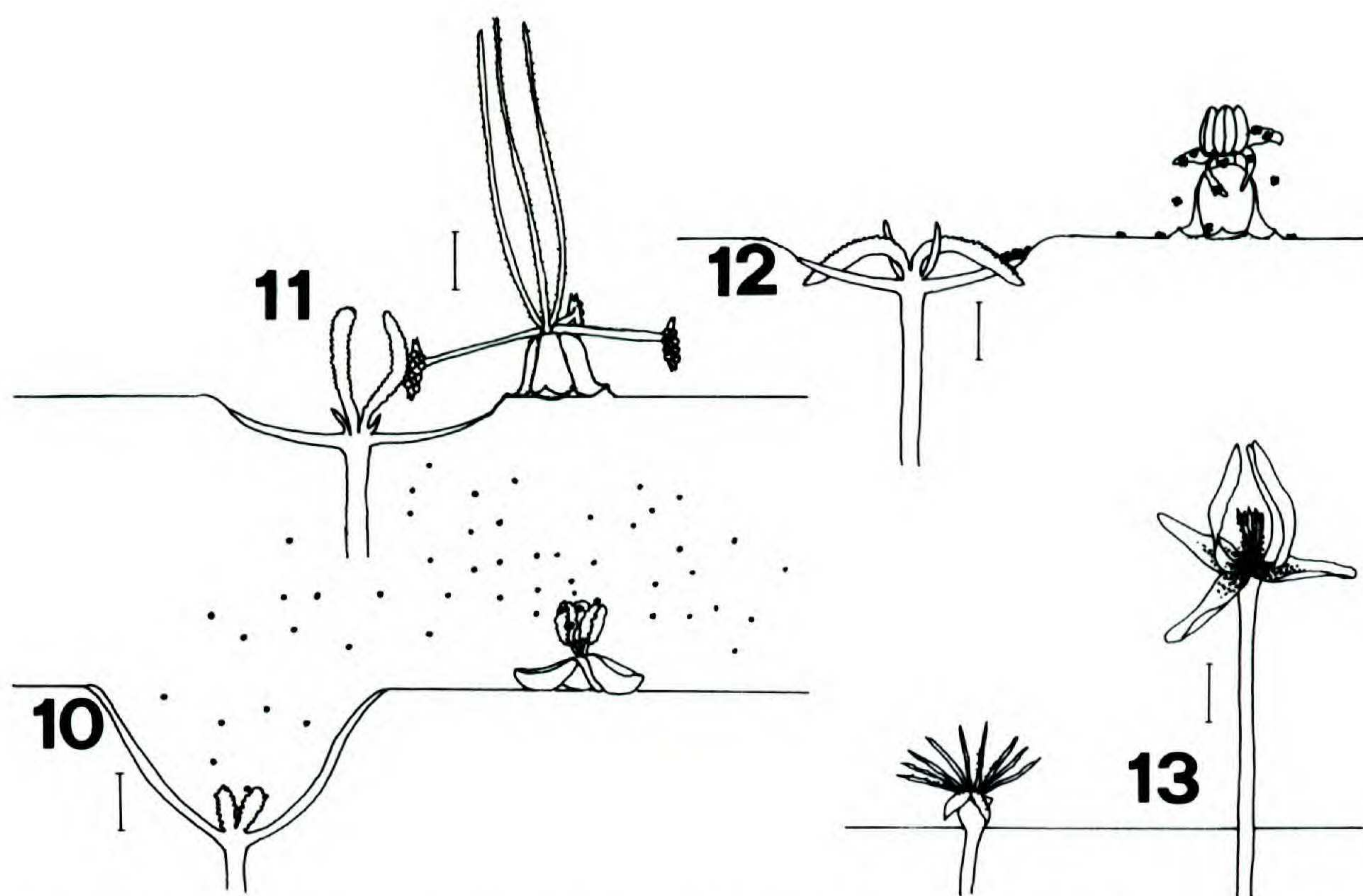
FIGURES 10–13.   10. *Diagram of pollination in* Hydrilla verticillata. *Left, female. Right, male. Scale bar =
0.8 mm.—11. Diagram of pollination in* Lagarosiphon muscoides. *Left, female. Right, male. Scale bar = 1.2
mm.—12. Diagram of pollination in* Elodea nuttallii. *Left, female. Right, male. Scale bar = 2 mm.—13. Diagram
of the flowers of* Limnobium laevigatum. *Left, female. Right, male. Scale bar = 3 mm.*
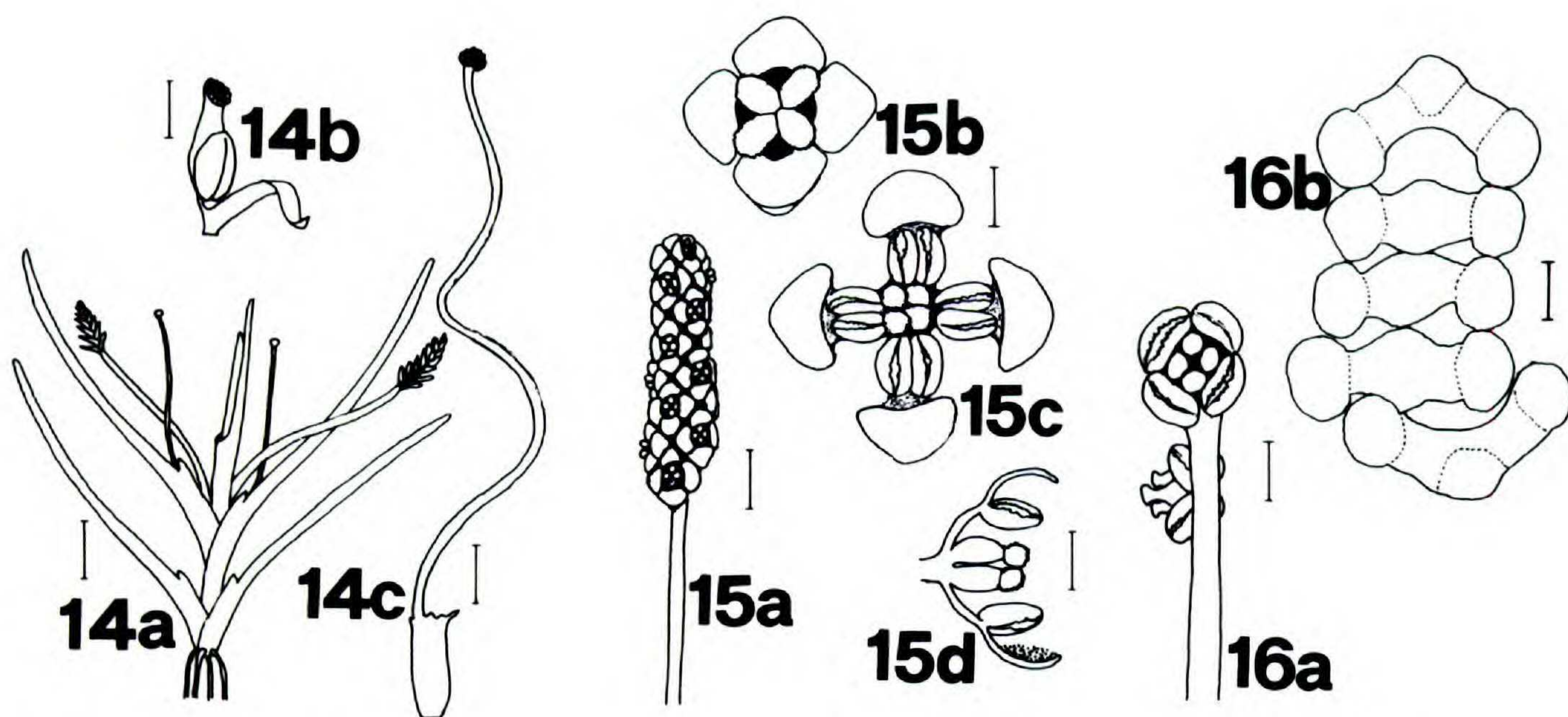
FIGURES 14–16.   14. *Diagrammatic representation of* Lilaea scilloides. *(a) Whole plant with inflorescences.
Scale bar = 8 mm. (b) Bisexual flower. Scale bar = 3 mm. (c) Long-styled, female flower. Scale bar = 5
mm.—15. Diagrammatic representation of* Potamogeton polygonifolius. *(a) Inflorescence during female phase.
Scale bar = 1 mm. (b) Flower at female phase. Scale bar = 1 mm. (c) Flower at male phase. Scale bar = 1
mm. (d) Longitudinal section of flower at male phase, showing the connective appendages as pollen arresting
organs. Scale bar = 1 mm.—16. Diagram of* Ruppia maritima. *(a) Inflorescence. Scale bar = 1 mm. (b) Chain
of five pollen grains. Scale bar = 20 μm.*
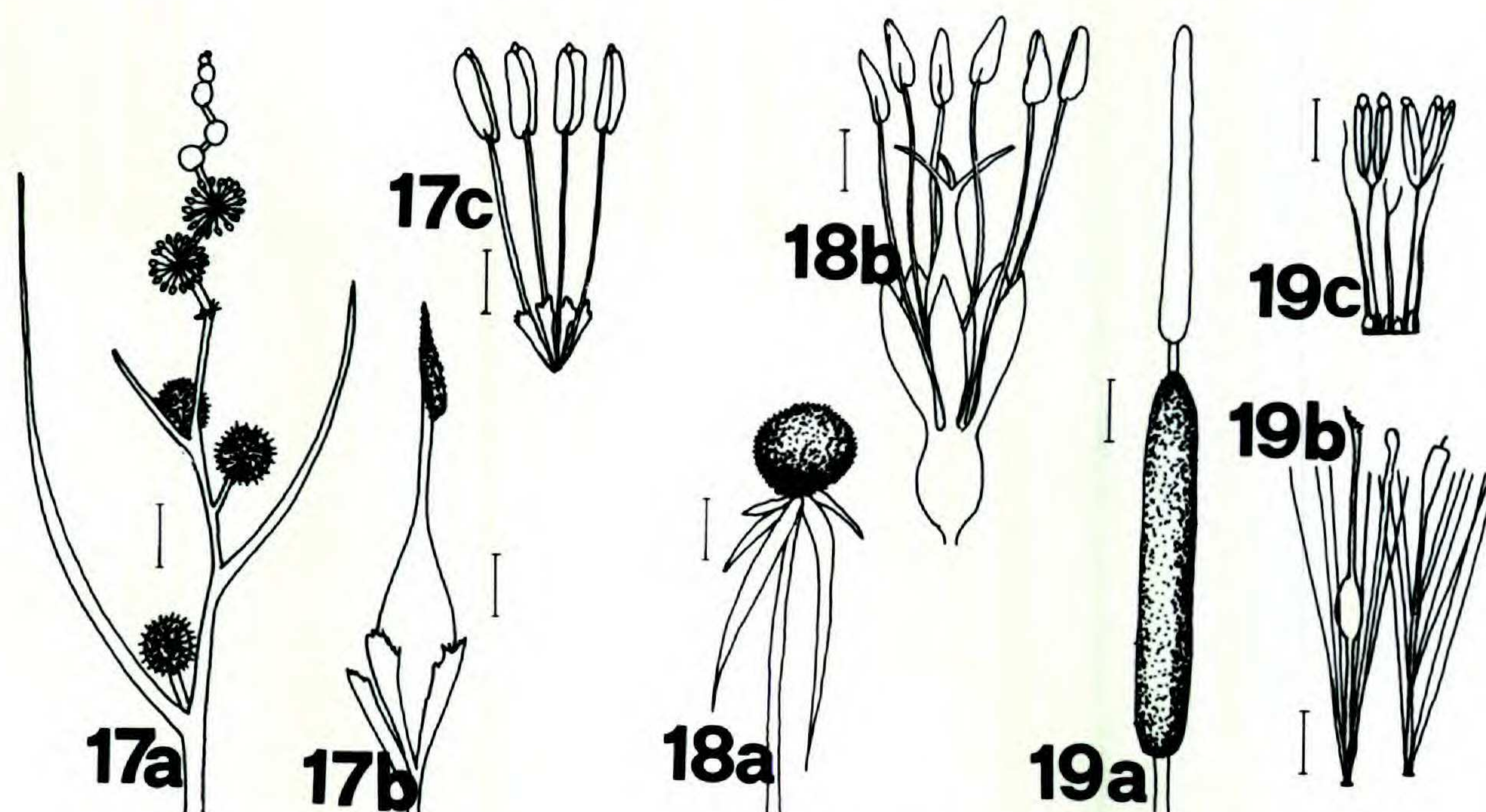
FIGURES 17-19.   17. *Diagrammatic representation of* Sparganium emersum. *(a) Inflorescence; male flowers above, females below. Scale bar = 2 cm. (b) Female flower. Scale bar = 1 mm. (c) Male flower. Scale bar = 1.5 mm.—18. Diagram of* Thurnia sphaerocephala. *(a) Inflorescence. Scale bar = 1 cm. (b) Flower. Scale bar = 0.8 mm.—19. Diagrammatic representation of* Typha angustifolia. *(a) Inflorescence; male above, female below. Scale bar = 2 cm. (b) Female flowers; left fertile, right sterile. Scale bar = 2 mm. (c) Male flowers. Scale bar = 1 mm.*

TYPHACEAE

This monotypic family is relatively well documented and is clearly wind pollinated (Fig. 19; see Krattinger, 1975), even though syrphid flies may collect pollen adhering to the female inflorescence.

All species have single ovules in each flower; some species, however, have pollen in tetrads. This contradicts all previous theoretical predictions regarding the function of pollen tetrads in pollination. Nicholls & Cook (1986) found that pollen tubes from tetrads are capable of traversing from the stigma of one flower through air to the stigma of another (Fig. 20) and fertilizing neighboring flowers. This results in increased efficiency of gametes in effecting fertilization (measured as seed-set) compared with other species of *Typha* having single pollen grains.

CONCLUSIONS

About 79 angiosperm families and 380 genera contain aquatic species. Most of the data are to be found in Cook et al. (1974). Excluding the Podostemaceae, because its floral biology is so poorly known, 31.6% of the families and 42% of the genera are pollinated abiotically.

Of the abiotically pollinated genera, 18 (or 19 including *Potamogeton*) have wettable pollen and are pollinated under water; about seven genera are

pollinated at the water surface. This leaves 119 genera (35.5%) exclusively wind pollinated. I have tried without success to find geographical correlations between pollination and distribution of aquatics; it seems that about one-third wind pollinated remains reasonably constant when one compares the Old and New worlds, Northern and Southern hemispheres, and Tropics and Temperate zones. Within particular plant communities or associations there are enormous differences in the proportion of wind-pollinated species as also found by Kugler (1971). Reedswamp and sedge-dominated communities are mostly made up of wind-pollinated plants. Also the plants of deep and permanent water are mostly abiotically pollinated; all the marine angiosperms, for example, are hydrogamous. Nevertheless, about two-thirds of all aquatic genera (and this probably also applies at the level of species) are biotically pollinated.

So little is known about the breeding systems of aquatic species that it is not possible to generalize on in- or outbreeding within the context of the mode of pollination.

Aquatic angiosperms have evolved from terrestrial ancestors. All available evidence suggests that the aquatic members of at least six families (Centrolepidaceae, Cyperaceae, Hydatellaceae, Juncaceae, Plantaginaceae, and Poaceae) have evolved from anemophilous ancestors. This translates to an
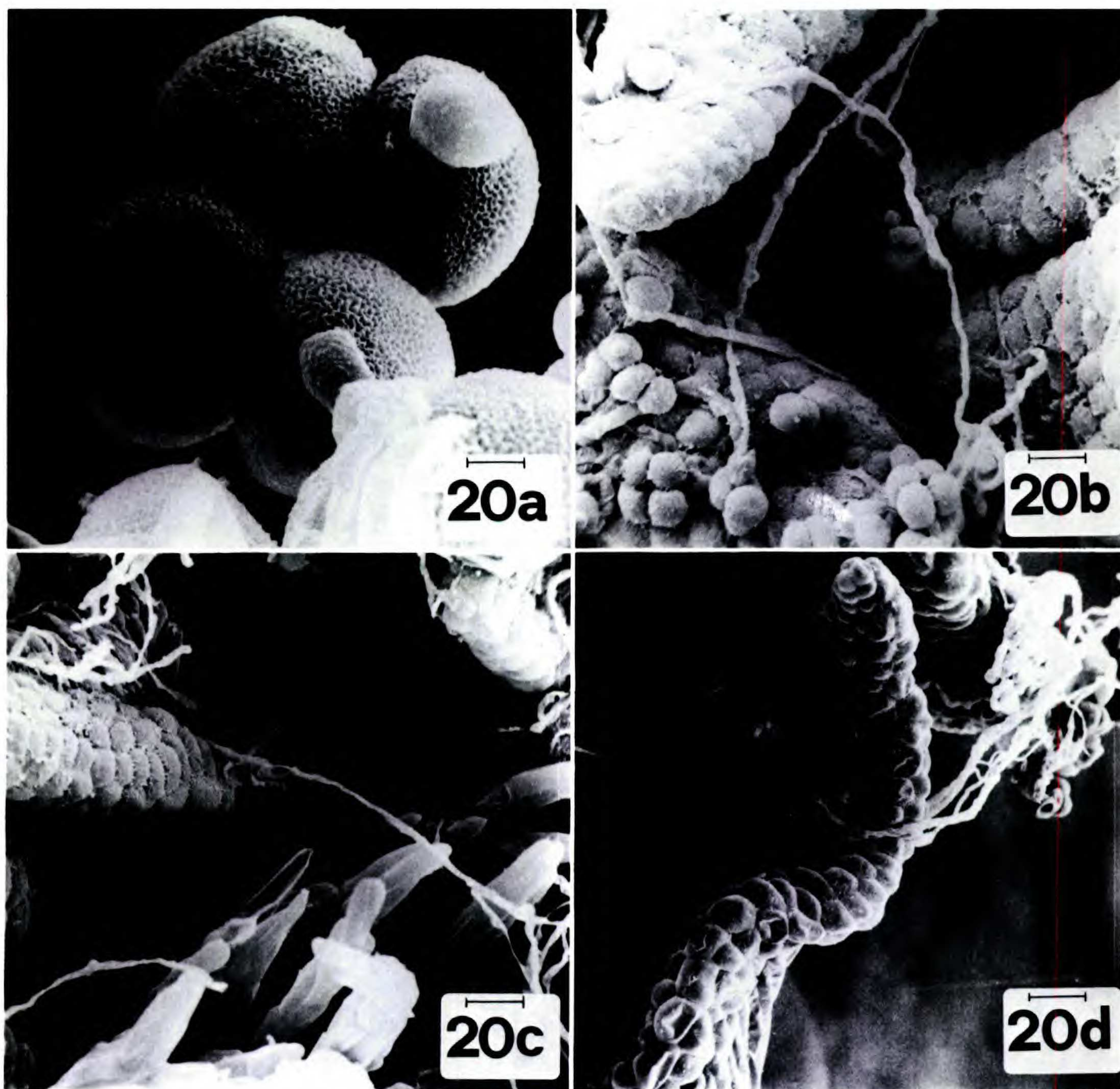
FIGURE 20. Typha latifolia.—a. Pollen tetrad, two grains germinating. Scale bar = 5 μm.—b–d. Pollen tubes crossing from one stigma to another. b, scale bar = 3 μm; c, d, scale bar = 50 μm.

estimate of at least 100 genera that brought anemophily with them into the aquatic milieu. This leaves a mere 19 genera where the anemophily may have evolved subsequent to the invasion of the aquatic habitat. When these 19 genera are examined a little closer, although they do not have any obvious terrestrial relatives, they mostly belong to exclusively anemophilous families (Callitrichaceae, Haloragaceae, Hippuridaceae, Hydrostachydaceae, Lilaeaceae, Potamogetonaceae, Ruppiaceae, Sparganiaceae, Thurniaceae, and Typhaceae).

In only *Brasenia* (Cabombaceae) and *Limnobium* (Hydrocharitaceae) is it very likely that the evolution from entomophily to anemophily has taken place in the aquatic environment. The genus *Hydrilla* (Hydrocharitaceae) is not strictly "wind" pollinated, because heavy pollen grains are actively propelled from the male flowers to the females. This mechanism relies on water and therefore probably evolved in water. However, it shows an alternative pathway to the evolution of anemophily.

From a total of 380 aquatic angiosperm genera, a minimum of two and a maximum of 19 may have evolved from entomophily to anemophily subsequent to the invasion of the aquatic habitat. From these numbers alone it does not seem likely that pollination by wind is a feature that is especially associated with life in the aquatic environment like, for example, the presence of gas spaces (lacunae) and hydropoten or the absence of lignin and/or stomata. Many aquatics clearly evolved from ter-

restrial groups that were already anemophilous; there is no evidence that any of these aquatics have returned to biotic pollen transfer. Taken as a whole, it is not possible to say that anemophily is particularly beneficial or detrimental to plants living in water. However, it is remarkable, when the different floral types illustrated in this contribution are compared, how many different strategies are adopted to guarantee transference of pollen by means of wind. There are no obvious trends among the wind-pollinated aquatics that indicate the pathway to hydrogamy. "Aquatic" anemophily is not different from "terrestrial" anemophily.

LITERATURE CITED

BRUGGEN, H. W. E. VAN. 1985. Monograph of the genus *Aponogeton* (Aponogetonaceae). Biblioth. Bot. 137: 1–76.

COOK, C. D. K. 1982. Pollination mechanisms in the Hydrocharitaceae. Pp. 1–15 *in* J.-J. Symoens, S. S. Hooper & P. Compère (editors), Studies on Aquatic Vascular Plants. Royal Botanical Society of Belgium, Brussels.

——— & R. LÜÖND. 1982. A revision of the genus *Hydrilla* (Hydrocharitaceae). Aquatic Bot. 13: 485–504.

——— & ———. 1983. A revision of the genus *Blyxa* (Hydrocharitaceae). Aquatic Bot. 15: 1–52.

——— & M. S. NICHOLLS. 1986. A monographic study of the genus *Sparganium* (Sparganiaceae), Part 1. Subgenus *Xanthosparganium* Holmberg. Bot. Helvet. 96: 213–267.

——— & ———. 1987. A monographic study of *Sparganium* (Sparganiaceae), Part 2. Subgenus *Sparganium*. Bot. Helvet. 97: 1–44.

——— & K. URMI-KÖNIG. 1983. A revision of the genus *Limnobium* including *Hydromystria* (Hydrocharitaceae). Aquatic Bot. 17: 1–27.

——— & ———. 1985. A revision of the genus *Elodea* (Hydrocharitaceae). Aquatic Bot. 21: 111–156.

———, R. LÜÖND & B. NAIR. 1981. Floral biology of *Blyxa octandra* (Roxb.) Planchon ex Thwaites (Hydrocharitaceae). Aquatic Bot. 10: 61–68.

———, B. J. GUT, E. M. RIX, J. SCHNELLER & M. SEITZ. 1974. Water Plants of the World. W. Junk, The Hague.

CRANE, P. R. 1986. Form and function in wind dispersed pollen. *In:* S. Blackmore & I. K. Ferguson (editors), Pollen and Spores. Academic Press, London. Symposium Series, Number 12: 179–202.

CUSSET, C. 1973. Révision des Hydrostachyaceae. Adansonia 13: 75–119.

DAHLGREN, R. M. T., H. T. CLIFFORD & P. F. YEO. 1985. The Families of the Monocotyledons. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.

KRATTINGER, K. 1975. Genetic mobility in *Typha*. Aquatic Bot. 1: 57–70.

KUGLER, H. 1971. Die Verbreitung der Anemogamie in mitteleuropäischen Pflanzengesellschaften. Ber. Deutsch. Bot. Ges. 84: 197–209.

LANDOLT, E. 1986. The family of Lemnaceae—a monographic study, Volume 1. Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich 71: 1–566.

NICHOLLS, M. S. & C. D. K. COOK. 1986. The function of pollen tetrads in *Typha* (Typhaceae). Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich 87: 112–119.

NIKLAS, K. J. 1985. The aerodynamics of wind pollination. Bot. Rev. (Lancaster) 51: 328–386.

PATTEN, B. C. 1956. Notes on the biology of *Myriophyllum spicatum* L. in a New Jersey lake. Bull. Torrey Bot. Club 83: 5–18.

PHILBRICK, C. T. 1984a. Pollen tube growth within vegetative tissue of *Callitriche* (Callitrichaceae). Amer. J. Bot. 71: 882–886.

———. 1984b. Aspects of floral biology, breeding system, and seed and seedling biology in *Podostemum ceratophyllum* (Podostemonaceae). Syst. Bot. 9: 166–174.

POHL, F. 1937a. Untersuchungen zur Morphologie und Biologie des Pollens IV. Die Pollenerzeugung der Windblütler. Beih. Bot. Centralbl. 56A: 365–470.

———. 1937b. Beiträge zur Morphologie und Biologie des Pollens VII. Die Pollenkorngewichte einiger windblütiger Pflanzen und ihre ökologische Bedeutung. Beih. Bot. Centralbl. 57A: 112–172.

POSLUSZNY, U., W. A. CHARLTON & D. K. JAIN. 1986. Morphology and development of the reproductive shoots of *Lilaea scilloides* (Poir.) Hauman (Alismatidae). Bot. J. Linn. Soc. 92: 323–342.

SCHOTSMAN, H. D. 1982. Biologie florale des *Callitriche*: étude sur quelques espèces d'Espagne méridionale. Bull. Mus. Natl. Hist. Nat., 4e Sér., Sect. B, Adansonia 4: 111–160.

———. 1985. Biologie florale des *Callitriche* (Callitrichaceae): II. Etude sur quelques espèces d'Océanie. Bull. Mus. Natl. Hist. Nat., 4e Sér., Sect. B, Adansonia 7: 357–375.

SCULTHORPE, C. D. 1967. The Biology of Aquatic Vascular Plants. E. Arnold, London.

SIVADASAN, M. 1986. *Wiesnéria triandra* (Dalzell) Micheli, eine sehr seltene und wenig bekannte Alismatacee aus Indien. Aqua-Planta 86: 159–161.

STELLEMAN, P. 1984. Reflections on the transition from wind pollination to ambophily. Acta Bot. Neerl. 33: 497–508.

STÜTZEL, T. 1981 [1982]. Zur Funktion und Evolution köpfchenförmiger Blütenstände, insbesondere der Eriocaulaceae. Beitr. Biol. Pflanzen 56: 439–468.

———. 1984. Blüten- und infloreszenzmorphologische Untersuchungen zur Systematik der Eriocaulaceen. Diss. Bot. (Vaduz) 71: 1–108.

VERHOEVEN, J. T. A. 1979. The ecology of *Ruppia*-dominated communities in western Europe. I. Distribution of *Ruppia* representatives in relation to their autecology. Aquatic Bot. 6: 197–267.

WHITEHEAD, D. R. 1969. Wind pollination in the angiosperms. Evolution 23: 28–35.

YEO, R. R., R. H. FALK & J. R. THURSTON. 1984. The morphology of hydrilla (*Hydrilla verticillata* (L. F.) Royle). J. Aquatic Pl. Managem. 22: 1–16.